Allometric scaling of the extinction vortex

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Summary

Previous work has demonstrated that a multitude of stressors acting synergistically on small populations can lead to a self-reinforcing downward spiral to extinction known as the extinction vortex. However, owing to a lack of studies, we currently have a poor understanding of what factors might affect how a population responds to the extinction vortex and therefore, the relative immediacy or intensity of conservation intervention required to save extinction-bound populations. In this thesis, I compile a dataset of 55 populations monitored to extirpation, test three pre-existing hypotheses of the extinction vortex, and investigate whether a key fitness-related phenotypic trait - body size - influences the population dynamics in the region of extinction. In support of extinction vortex theory, I find that time to extinction scales to the logarithm of population size, geometric growth rate becomes increasingly negative at closer proximity to extinction, and there is greater variability in geometric growth rate as populations approach extinction. I also find that the relationship between population size and population longevity is weaker for smaller-bodied taxa. This indicates a predisposition for more abrupt extinctions in smaller-bodied species and a stronger decline to extinction in larger-bodied species, which might be more difficult to reverse with conservation effort. Overall, the ability to predict how population size scales to population longevity based on the intrinsic biological traits of taxa could have implications for conservation management.

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Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED:

DATE:

Declaration of co-authorship

Chapter two is based on a co-authored manuscript, which has been edited for the purpose of use in this thesis. However, it was authored by the student with no more input from co-authors or supervisors than would have been provided in drafting a conventional thesis chapter.

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Chapter 1: General Introduction

1.1 The sixth mass extinction

Extinction, defined as the loss of all constituents of a population or species (Ladle & Jepson 2008), seems to be an inevitable occurrence for all species; less than 1% of all species that have ever existed are still extant (Raup 1986). Furthermore, the fossil record demonstrates that across time, periods of low rates of extinction are occasionally disrupted by sudden pulses of extinction – so-called mass extinction events – in which at least 75% of species go extinct in a relatively short period of time (~1-2 million years) (Raup & Seposki 1982). Over the past 500 million years, five of these mass extinction events have been documented (Raup 1986); the most recent occurring ca66 million years ago (Cretaceous-Tertiary), and by far the largest occurring ca251 million years ago (Permian-Triassic), responsible for the loss of over 96% of species (Sahney & Benton 2008).

There is concern that the current anthropogenic impact on the biosphere is so great that it has triggered the start of the next mass extinction event (Dirzo et al. 2014; Ceballos et al. 2015). Accordingly, a new geological epoch has been postulated: 'the Anthropocene' (Lewis & Maslin 2015), in which the functions of global ecosystems are predominantly influenced by humanity. As anthropogenic activity continues to drive the contraction of populations of species worldwide, it is becoming increasingly important to understand the causes of biodiversity loss, its potential consequences, and how we as a global society might be able to reverse the current trend.

1.2 Causes of biodiversity loss

1.2.1 The five main drivers

Biodiversity is normally conceptualised at three levels of biological organisation. *Genetic diversity* refers to the total amount of genetic variation between individuals within a population, species or community. *Species diversity* is the total number of species living at a particular location. *Ecosystem diversity*, the highest level of biodiversity, is defined as the total number of ecosystems in a certain area. All three levels of biodiversity are of concern

to conservationists; however, this thesis is focused on biodiversity loss at the level of species.

Understanding the drivers of biodiversity loss is critical if we are to minimise extinctions into the future. Broadly, anthropogenic drivers of biodiversity loss can be categorised into five groups (Young et al. 2016): i. a *warming climate*, resulting from a massive increase in greenhouse gas emissions following the onset of the industrial revolution, which is a direct stressor to species in itself (Spooner et al. 2018) and is a cause of other stressors such as more frequent extreme weather events, forest fires and a rise in sea-levels (IPCC 2014); ii. the omnipresence of persistent *pollutants* (e.g. plastics, sound, light and organic and inorganic chemicals) (Longcore & Rich 2004; Slabbekoorn & Ripmeester 2008; Barnes et al. 2009; Rhind 2009), even in the world's most remote areas (Dasgupta et al. 2018); iii. the intentional or incidental transmission of species across continents, leading to the widespread prominence of *invasive species* in all ecosystems (Mack et al. 2000); iv. the intentional or incidental *habitat loss* due to destruction of some of the world's richest biomes, such as rainforests and coral reefs (Foley et al. 2005; Hoegh-Guldberg et al. 2007); v. relentless *overexploitation* of organisms for consumption (Fa et al. 2002; Ripple et al. 2016), various uses of body parts (Rosen & Smith 2010) or due to human-wildlife conflict (Shaffer et al. 2019), causing a direct reduction in population numbers.

It is common for species to be threatened by multiple stressors, with interactions between them potentially accelerating the rate of decline (Brook et al. 2008). Disturbingly, the 2018 Living Planet Report estimated that, on average, wild vertebrate populations have declined by 60% since 1970 (WWF 2018). Moreover, according to the 'small population paradigm', as populations diminish in size, they become increasingly vulnerable to a suite of additional processes (Caughley 1994).

1.2.2 The small population paradigm

Theoretical and empirical advances have substantially improved our understanding of the mechanisms underpinning how populations decline to extinction. Deleterious processes inherent to small populations can inexorably lead to the local extinction of a population of a

species in a geographic area, a process known as extirpation (Caughley 1994; Brook et al. 2008). These processes can be broadly separated into three well-accepted categories i. demographic effects, ii. genetic effects and iii. environmental stressors (Griffen & Drake 2008).

Demographic stochasticity, driven by the semi-random processes of reproduction and death between individuals (Gilpin & Soulé 1986), becomes increasingly important in smaller populations as the fate of an individual has a proportionally greater impact on the populations' dynamics and abundance (Caughley 1994). For example, in the declining Doñana population of Iberian lynx (*Lynx pardinus*), demographic stochasticity appears to have resulted in a female-biased sex ratio impairing the populations' ability to recover (Palomares et al. 2012). *Allee effects* are other demographic processes resulting from a decline in individual fitness, following a reduction in population size (Courchamp et al. 1999). For example, a reduced population size makes locating a mate and reproduction less likely and cooperative hunting or anti-predator behaviour becomes less efficient in smaller aggregations (Berec et al. 2007). A contemporary type of Allee effect concerns anthropogenic harvesting of rare species; as a species becomes rarer its market value increases, driving even more intense harvesting (Courchamp et al. 2006).

Genetic stochasticity (also termed 'genetic drift') is the random temporal fluctuation in allele frequencies between generations, influencing the level of genetic diversity. This process is especially important in small populations, where the chance of the fixation of deleterious alleles is greater, reducing individual fitness and limiting the ability of a population to adapt (Lynch et al. 1995; Frankham et al. 1999). *Inbreeding*, results from the mating of closely related conspecifics and is more likely in small populations (Tanaka 2000). The consequences of inbreeding are akin to that of genetic drift; a rise in homozygosity leading to a reduction in population fitness and adaptability (inbreeding depression) (Lynch et al. 1995; Caughley 1994; Pimm et al. 2005), enhancing extinction risk (Sacherri et al. 1998). The negative effects of the loss of genetic diversity in wild populations have been frequently reported; the Florida panther (*Puma noncolor coryi*) suffered significantly elevated rates of genetic defects as a result of population contraction (Pimm et al. 2005), though the situation improved following the introduction of eight individuals from a

separate population, which alleviated inbreeding depression and reversed the declining population trend (Johnson et al. 2010). Likewise, the greater prairie chicken (*Tympanuchus cupido pinnatus*) underwent a catastrophic decline from 1962-1994, and individual reproductive rate decreased despite favourable environmental conditions (Westemeier et al. 1998). Also, individual survival and reproductive rate declined in the Iberian lynx (*Lynx pardinus*) (Palomares et al. 2012) and southern dunlin (*Calidris alpina*) (Blomqvist et al. 2009) following population contraction and a corresponding increase in homozygosity. The negative implication of genetic decay on extinction risk is also evidenced by the fact that heterozygosity of non-threatened taxa is greater than that of threatened sister taxa (Spielman et al. 2004).

Environmental stochasticity, arising from external factors such as anthropogenic activities (i.e. the five main stressors detailed above) or natural environmental variation (i.e. weather), directly or indirectly drive birth and death rates (Gilpin & Soulé 1986). Unlike demographic stochasticity, environmental stochasticity is not a consequence of small population size but the implications for persistence is greater for smaller populations. Famously, a size-selective increase in mortality was demonstrated in the medium ground finch (*Geospiza fortis*), following two droughts from 1976-77 and 1984-86 (Grant & Grant 1994). The most extreme environmental events, *catastrophes*, can cause the direct and sudden eradication of a small population; the Bramble Cay melomys (*Melomys rubicola*) is believed to have been rendered extinct following extreme weather events (Watson 2016).

1.2.3 The extinction vortex

Among the stressors to which small populations are exposed, it is unlikely that the extirpation of a population can be exclusively attributed to a single one (Figure. 1.1). Rather, the assortment of stressors outlined above are almost certainly going to occur simultaneously, with the interaction between them exacerbating the rate of population decline. Accordingly, the concurrent presence of these stressors is postulated to result in self-reinforcing downward spirals to extinction – so-called ‘extinction vortices’ (Gilpin & Soulé 1986).

For a conceptual example of how the manifold stressors combine to result in an extinction vortex, imagine a species of ground-dwelling rainforest bird. Across its range, anthropogenic deforestation has fragmented its habitat producing smaller, isolated populations that are still stable. However, in one location, the population experiences a population bottleneck due to a drought. The bottleneck has severely compromised the genetic diversity of the population, leaving it ill-equipped to cope with the introduction of a foreign-infectious disease transmitted from closely related domestic livestock, leading to a further reduction in population size. The now critically low population is under acute risk of demographic stochasticity and Allee effects. As such, none of the individuals successfully reproduce in the following year and the population does not replace the individuals lost through natural causes and direct harvesting by humans, reducing the population to a mere few individuals. Finally, the extirpation of the population is brought about by a forest fire.

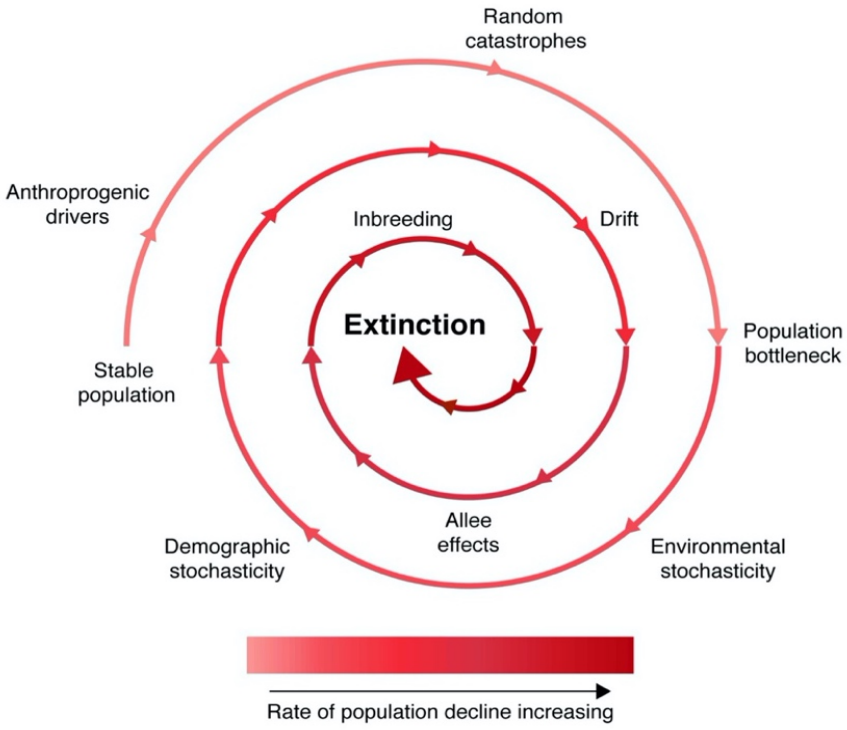

Figure 1.1 A schematic representation of the extinction vortex.

Three key predictions of extinction dynamics emerge from the extinction vortex. First, the proximity to extinction is expected to become increasingly small as population size diminishes, therefore time to extinction should scale to the logarithm of population size

(Lande 1993; Fagan & Holmes 2006). Second, Allee effects and the reduction of heterozygosity in smaller populations, means that individual fitness is expected to decline with population size and at closer proximity to extinction. This should manifest in greater rates of annual geometric decline as population size decreases and as the proximity to extinction becomes closer (Fagan & Holmes 2006). Third, dwindling populations are much more impacted by demographic stochasticity (Gilpin & Soulé 1986; Caughley 1994; Benson et al. 2019); if stochastic processes are involved in the final extinction, annual variability is expected to become greater at closer proximity to extinction (Fagan & Holmes 2006). Corroboration of these predictions was found in 10 wild vertebrate populations monitored to extirpation (Fagan & Holmes 2006).

1.3 Consequences of biodiversity loss

The global decline in biodiversity is severely compromising the ability for ecosystems to function, with significant implications for life on earth, including human life (Ceballos et al. 2017). This is because degraded ecosystems do not provide the multi-faceted benefits, collectively termed 'ecosystem services' (MEA 2003; Holzman 2012), inherent to intact ecosystems and that support global economies (Costanza et al. 1997) and human health (MEA 2003). Furthermore, though difficult to quantify, the intrinsic value of biodiversity to humans and how it inspires cultural practices should not be underestimated (Daniel et al. 2012).

It is increasingly apparent that the loss of just a single species from an ecosystem can completely destabilise the community, drastically altering its structure and composition. These so-called 'trophic cascades' have been recorded in most of the world's biomes and are associated with the loss of large-bodied species at the highest trophic levels (Ripple et al. 2014). In fact, some of the most important species for ecosystem function, often referred to as 'keystone species', are also among the most globally endangered (Ripple et al. 2014). The deleterious side-effects of these trophic cascades for humans is exemplified by the dramatic increase in rabies cases following the catastrophic decline of the local vulture populations in India (Kareiv & Marvier 2007; Markandya et al. 2008).

Given that human prosperity seems to be contingent on biodiversity (Naeem et al. 2012; Ehrlich & Ehrlich 2013; Dirzo et al. 2014), if unabated, it is certain that the ongoing loss of biodiversity will have dire consequences (Ceballos et al. 2017; Ceballos et al. 2020). Recognising how important the health of the biosphere is to humanity should provide strong impetus for societies to conserve their environment (Kareiv & Marvier 2007).

1.4 Conservation priorities

Given its importance, the preservation of biodiversity has become a key political agenda; for example, it is the primary target of the Convention on Biological Diversity (CBD 2018). Despite this, funding for conservation activities is not unlimited, therefore it is necessary to prioritise effort in such a way as to minimise the loss of biodiversity in the most cost-effective manner (Myers et al. 2000; Arponen 2012). Specific criteria that may determine the effectiveness of conservation activities, and that should be considered during the allocation of resources, have been identified (Arponen 2012): i) species value, ii) species threat level and iii) species salvageability. Whilst existing schemes of species prioritisation tend to focus disproportionately on the threat level of species (criteria 2), some have emphasised that relying exclusively on threat status is not the most efficient way in which to minimise extinction (Possingham et al. 2002). A species that is highly valuable to the ecosystem, is threatened with extinction and has the potential to respond positively to conservation intervention, should preferentially receive conservation attention (Marsh et al. 2007).

1.4.1 Assigning value to species

Some species hold particularly high economic or cultural importance, with high-profile conservation programs sometimes devoted to these 'flagship species', as epitomized by the conservation of the giant panda (*Ailuropoda melanoleuca*) (Wei et al. 2018). Ironically, focusing on a single species may also be an effective way of preserving whole communities, as conserving the habitat of the flagship species benefits all other species living in sympatry. Conserving these flagship or 'umbrella' species may be the most effective option in some areas, because information on the status of all organisms in a community is often not available. However, given the disparate ecology among co-occurring species, prioritising

particular species does not guarantee benefits to all species under the umbrella; in this way, prioritising umbrella species does not provide a silver-bullet solution (Roberge & Angelstam 2004).

Alternatively, we can assign value to species more systematically, by explicitly quantifying the contribution of a given species to phylogenetic diversity or to ecosystems. For example, we might aim to maximise the preservation of unique traits and evolutionary history by prioritising species based on their phylogenetic distinctiveness (Arponen 2012). A real-life implementation of this is with so-called 'Evolutionarily Distinct and Globally Endangered' (EDGE) species; those that are both evolutionarily distinct and under exceptionally high risk of extinction (see below) (Isaac et al. 2007; Collen et al. 2011). This is the basis for the *'EDGE of Existence Programme'* which aims to draw attention to the species with the highest EDGE ranking. However, evolutionarily distinct (or 'relict') lineages may be less likely to contribute to future diversity. Also, due to convergent evolutionary processes, evolutionary uniqueness does not necessarily serve as a proxy for ecological uniqueness (Arponen 2012). This is important as the integrity of an ecosystem is dictated by the communities' ability to occupy a diverse array of niches, rather than the degree of taxonomic diversity, per se (Gagic et al. 2015; Lefcheck & Duffy 2015). Functionally Unique, Specialised and Endangered (FUSE) species are akin to EDGE species in that they are globally endangered, but they are also ranked according to the uniqueness of their combination of traits and, therefore, how distinct their role is in the ecosystem (Pimiento et al. 2020). In theory, the loss of higher-ranking FUSE species will have the greatest consequences for the ecosystem, meaning they should be preferentially considered for conservation activities.

1.4.2 Assigning threat level to species

Key to the appropriate designation of conservation priorities, is the categorisation of species according to their extinction risk. In and of themselves, metrics of rarity (e.g. geographic range size, habitat breadth and local abundance) are not necessarily good surrogates of extinction risk; naturally rare species can persist longer than abundant species if the latter has a rapidly declining population trend (Arponen 2012; Mace et al. 2008). Furthermore, certain forms of rarity may be inherently better predictors of persistence than others

(Harnik et al. 2012). Therefore, a more complete measure of extinction risk is one that encapsulates multiple symptoms of threat (i.e. low population size, declining population trend and small range size). The recognition of this and the need for a reputable, accessible index of extinction risk that is applicable to all species led to the development of the International Union for the Conservation of Nature Red List of Threatened Species (IUCN Red List); now the most widely accepted system of quantifying species extinction risk (Mace et al. 2008).

The IUCN Red List categorises species as 'extinct', 'threatened' or 'non-threatened'. Sub-categories of 'threatened' (vulnerable, endangered and critically endangered) are designated according to five independent criteria and represent the probabilistic chance of extinction, with more 'critically endangered' species expected to go extinct in a given time frame than 'endangered' or 'vulnerable' species (Mace et al. 2008). Non-threatened species, those that do not satisfy any of the criteria of threatened species, are classed as 'least concern' or 'near threatened'; the latter if the species only narrowly does not qualify as threatened. Over a quarter of species on the list are designated as threatened; however, the 120,372 species of animals, plants and fungi assessed to date (IUCN 2020), is still less than 10% of the total number of catalogued species in these groups (Mora et al. 2011). This is problematic, because highly threatened species with important ecosystem functions will escape the attention of conservationists.

Analysis of the distribution of extinction risk in vertebrate clades has demonstrated that risk is phylogenetically non-random (e.g. Gaston & Blackburn 1995), which has two implications. First, it will lead to a greater loss of evolutionary history compared to if threat was randomly distributed across phylogenies (Purvis et al. 2000a; Johnson et al. 2002; Jones et al. 2003; Cardillo et al. 2006; Garcia et al. 2007). Second, it suggests that biodiversity loss can, at least in part, be explained by the species' biological traits (Bennett & Owens 1997; Purvis et al. 2000a). The latter is particularly interesting as biological traits that reliably correlate with extinction risk might be useful for conservationists to infer risk in the absence of more cryptic information such as population abundance or trend (O'Grady et al. 2004; Cardillo et al. 2008; Hilbers et al. 2016) and, in turn, address the shortfall in the number of species

assessed. Accordingly, many studies have sought associations between biological characteristics and extinction risk.

Life history speed

Life history speed is the tempo in which the major events in the lifetime of an organism occur, such as the age at maturity, reproductive output per breeding event and the number of breeding events per unit of time. Species with slow life history speeds naturally reproduce at a slower rate and, consequently, are less efficient at replacing individuals lost through perturbation (Bennett & Owens 1997; Purvis et al. 2000b; Brook & Bowman 2005; Werner & Griebeler 2011; Wang et al. 2019). The significance of life history speed in determining extinction risk may be contingent on threat type. For example, slower life history is reportedly linked to greater threat among species that are exploited, but not those threatened for other reasons (Owens & Bennett 2000; Price & Gittleman 2007). Likewise, during the Late Quaternary, species with slower life histories were more likely to be extirpated due to human hunting pressure (Johnson 2002). However, in farmland passerines threatened by habitat degradation, slower life histories actually seem to safeguard species possibly due to greater juvenile survival rate (Pocock 2010). Furthermore, this trait is also less important in groups that express limited variation in life history speed such as bats and primates (Purvis et al. 2000b; Jones et al. 2003; Safi & Kerth 2004).

Body size

Large body size is associated with many factors thought to increase extinction risk (Purvis et al. 2000b), including slow life history speeds (Johnson 2002; Brook & Bowman 2005; Sibly & Brown 2007; but see Isaac & Cowlishaw 2007; Hutchings et al. 2012). As such, large-bodied species are slower to respond to a loss of individuals and, as a consequence, are especially vulnerable to persecution and overexploitation by humans (Purvis et al. 2000b; Duncan et al. 2002; Fa et al. 2002; Brashares et al. 2003; Jerozolimski & Peres 2003; Isaac & Cowlishaw 2004; Cardillo et al. 2005; Ripple et al. 2016; Ripple et al. 2017); this is apparent from the numerous continental megafaunal extinction events that occurred following global human dispersal (Alroy 2001; Kerr 2003; Burney & Flannery 2005; Crees et al. 2019) and a tendency for larger-bodied organisms to be most at risk in the present (Brook & Bowman 2005; Estes

et al. 2011; Dirzo et al. 2014; Ripple et al. 2019). Despite this, the relationship between body size and risk is not necessarily unidirectional. For example, small-bodied species are generally more vulnerable if the primary threat is habitat destruction or pollution, owing to smaller geographic range sizes (Beissinger 2000; Owens & Bennett 2000; Ripple et al. 2017). Additionally, medium-sized Australian mammals are more threatened, because they are predominantly ground-dwelling and occur in arid habitats where the effects of humans and introduced species have been most severe (Cardillo & Bromham 2001; Johnson et al. 2006; Johnson & Isaac 2009).

Activity timing and 'sleep-or-hide' behaviour

Diurnal species display traits that may increase extinction risk, such as sociality and large body size (Purvis et al. 2000b), as well as being favoured by hunters (Kuchikura 1988). Mammalian species that survived the Late Quaternary extinction event, despite having slow reproductive rates, were mostly either nocturnal or arboreal and therefore sheltered from the influence of humans (Johnson 2002).

Species exhibiting 'sleep-or-hide' behaviour (*sleep* = hibernation, aestivation torpor; *hide* = use of burrows and other chambers) are thought to benefit from using their refuges to evade hunters and persist through poor environmental conditions (Liow et al. 2008), thus lowering their extinction risk. This hypothesis is supported by comparative studies on extant mammals (Davidson et al. 2009; Liow et al. 2009).

Degree of specialisation

Specialist species are adapted to exploit a more limited range of dietary or habitat resources than generalist species. Although specialists may profit from short-term ecological benefits, they may be less adept at responding to environmental perturbation (Bonin 2011; Raia et al. 2016). High habitat specialisation is associated with higher risk in bats, primates and reptiles (Foufapoulos & Ives 1998; Harcourt et al. 2002; Sagot & Chaverri 2015), whilst high dietary specialisation is associated with shorter species durations in North American canids (Balisi et al. 2018), increased rarity in primates (Harcourt et al. 2002) and greater threat category in bats (Safi & Kerth 2004; Boyles & Storm 2007). Importantly, whether degree of

specialisation influences risk also seems to depend on the predominant threat facing a taxon. For example, a high degree of specialisation is more likely to enhance extinction risk in species that are threatened by habitat loss (Owens & Bennett 2000; Isaac & Cowlishaw 2004), rather than persecution or invasive species, because only the former diminishes niche availability (Owens & Bennett 2000; Fisher et al. 2003).

Geographic range size & island endemism

It is frequently reported that geographic range size, the total area occupied by a species, is correlated with IUCN Red List category; species with smaller geographic range sizes are generally more threatened (Purvis et al. 2000b; Johnson et al. 2002; Jones et al. 2003; Cardillo et al. 2004; Price & Gittleman 2007; Cardillo et al. 2008; Chichorro et al. 2019). Although there is a potential circularity problem, as geographic range size is part of the index's criteria (Mace et al. 2008), this relationship nevertheless persists after excluding species listed as threatened due to small geographic range size (Jones et al. 2003; Cardillo et al. 2008; Lee & Jetz 2011). Indeed, geographic range size is correlated with attributes that might safeguard species from extinction such as population size (Pyron 1999), genetic diversity (Doyle et al. 2015) and niche breadth (Purvis et al. 2000b; Birskis-Barros et al. 2019; Chichorro et al. 2019).

Species that are endemic to islands generally have extremely restricted geographic ranges and, as a consequence, are often severely threatened (Purvis et al. 2000b; Sagot & Chaverri 2015). Due to their isolation, island endemics are more susceptible to invasive species (Savidge 1987) and foreign infectious diseases (Wyatt et al. 2009). Strikingly, around 80% of recorded extinctions since 1500AD were island endemics (Ricketts et al. 2005).

Home range size

Home range size is the average minimum area required by an organism to satisfy all of its resource requirements. A small home range size serves as an indication of a narrow habitat breadth, poor ecological flexibility and possibly small geographic range size (Pyron 1999). However, large home range size implies large body size, therefore slower life history speeds (Davidson et al. 2009) and low population densities (Fa & Purvis 1997). Also, species that

have larger home range sizes may be more likely to encounter the edges of nature reserves, where 'edge-effects' drive mortality (Brashares et al. 2003). In 10 large carnivore species, home range size was positively correlated with 'critical reserve size' (the reserve area required for a 50% probability of persistence), indicating that species with larger home range sizes are more vulnerable to extinction if the primary threat is habitat loss (Woodroffe & Ginsberg 1998). However, as a sole predictor, many studies have not found a significant relationship between home range size and extinction risk (Purvis et al. 2000b; Cardillo 2003; Price & Gittleman 2007).

Degree of Sociality

The fitness of individuals may depend on the presence of conspecifics, even though they are direct competitors for resources (Courchamp et al. 1999; Stephens et al. 1999). Social species that engage in group defence and foraging are thought to attain highest fitness at the optimum group size and may be particularly sensitive to the loss of conspecifics (Stephens et al. 1999). Species that form particularly large social groups require more resources and may be especially perturbed by habitat loss (Isaac & Cowlishaw 2007). For example, the once superabundant and hyper-gregarious passenger pigeon (*Ectopistes migratorius*) underwent a cataclysmic decline to extinction at the start of the 20th century (Halliday 1980). After years of intense harvesting and habitat loss, eventually a paucity of conspecifics is thought to have driven the species to extinction (Halliday 1980). However, out of 11 intrinsic and ecological traits, sociality was found to be the least important in determining mammalian extinction risk (Davidson et al. 2009), and no group size effect was found in several specific clades (Purvis et al. 2000b; Jones et al. 2003; Isaac & Cowlishaw 2007; Price & Gittleman 2007). One interpretation of these results is that behavioural plasticity in social species can, to a certain extent, buffer against a loss of individuals.

Trophic level

Species at higher trophic levels normally depend on less abundant and more unstable food resources (Carbone et al. 1999), making them especially vulnerable to perturbations at lower trophic levels (Purvis et al. 2000b). Globally, carnivores also have lower population densities (Fa & Purvis 1997; Ripple et al. 2014), which is also independently associated with

greater extinction risk (Foufopoulos & Ives 1998; Cardillo et al. 2004). Shorter durations in the fossil record have been found for canids in North America, that showed a higher degree of carnivory during the Cenozoic (Van Valkenburgh et al. 2004). Also, comparative studies of extinction risk involving extant taxa indicate that species at higher trophic levels are more likely to be threatened (Purvis et al. 2000b).

Conclusion

Existing studies investigating the relationship between extinction risk and biological characteristics suggest that some basic predictions can be made; higher degrees of specialisation and smaller geographic range sizes generally confer greater extinction risk (Chichorro et al. 2019). However, it is also apparent that extinction risk is not a simple phenomenon; there are numerous ecological pathways to a high risk of extinction, resulting from the complex interaction between the type of threat and the species' biology (Beissinger 2000; Cardillo et al. 2003; Isaac & Cowlishaw 2007; Price & Gittleman 2007; Cardillo et al. 2008; Davidson et al. 2009; Collen et al. 2011; Murray et al. 2014; Ripple et al. 2017). Moreover, comparative studies on extinction risk seem to be most informative when applied to a narrow taxonomic and geographic scope (Fisher & Owens 2004; Cardillo & Meijaard 2012; Chichorro et al. 2019).

1.4.3 The prospect of saving endangered species

Borrowing a concept from emergency medicine, 'ecological triage' describes the decision-making behind a protocol of species prioritisation that balances the relative importance and urgency of conservation action with the prospect that the extinction risk in a species can be mitigated through intervention (Flather et al. 2011a). Clearly, it is not in the interest of conservation practitioners to unnecessarily invest resources in species that are secure, or fruitlessly attempt to save those that are already foredoomed.

The need to assess the likelihood that a population will persist into the future and to provide empirically-informed population targets is the motivation for studies relating to 'minimum viable population size' (MVP), often defined as the population size required to ensure a 99% probability of survival over 100 years or 40 generations (Shaffer 1981; Brook et al. 2008; Frankham et al. 2014).

Meta-analyses have generally converged on MVPs numbering in the thousands (Harcourt 2002; Brook et al. 2006; Traill et al. 2007, Traill et al. 2010). Despite this, there are plenty examples of species persisting and recovering from much lower levels (Garnett & Zander 2011); for example, the kakapo (*Strigops habroptilus*) has a population size numbering less than 200 individuals but has an increasing population trend thanks to intense conservation intervention (Jamieson & Allendorf 2012). However, theory suggests that the kakapo may have already lost the ability to respond to future environmental change (Traill et al. 2010). This is because, based on studies on population genetics, an effective population size (N_e) of 500 is necessary to ensure long-term survival through the preservation of population adaptability (Frankham et al. 2014). With a mean ratio of N_e to census population size (N_c) being 1:100, an N_c of 5000 has been suggested to be the universal MVP. Given the need to make rapid decisions with very little data for most species, some advocate for the adoption of this rule of thumb (Brook et al. 2006; Traill et al. 2007, Traill et al. 2010). This might be especially useful in developing countries that may be hindered by the lack of resources and a solid 'knowledge base' (Traill et al. 2010; Brook et al. 2011). Indeed, although met with some acrimony (Beissinger et al. 2011; Flather et al. 2011b; McCarthy et al. 2011), the founders of the Species Ability to Forestall Extinction ('SAFE') index suggest that conservation effort may be better directed towards species with population sizes closer to the postulated universal MVP of 5000 (Clements et al. 2011).

A key point of contention, obstructing the adoption of a universally accepted MVP threshold, is whether a population that has declined to a level below an effective size of less than 500 individuals has in fact lost its perpetual ability to adapt in face of environmental change and is ultimately destined to go extinct under any contingency (Garnett & Zander 2011; Jamieson & Allendorf 2012; Frankham et al. 2014). Moreover, there is a need to address the issue of whether we can reliably extrapolate N_e to N_c (Jamieson & Allendorf 2012; Frankham et al. 2014; Reed & McCoy 2014). Overall, our current understanding of the factors that lead to extinction is too crude to abandon species that have already fallen below a prespecified number of individuals.

1.5 Overview & aims

As discussed, a large body of research has amassed examining the correlations between metrics of extinction risk and species' biological traits. Correlates of extinction risk tell us

how sensitive a species is to deterministic drivers of population decline and how readily it can be reduced to a point at which the threat of extinction is acutely high (Brook et al. 2008). However, less well understood is the relationship between these traits and extinction susceptibility — the propensity for a population to go extinct having reached a critically low size; for example, only a few studies have investigated extinction susceptibility in the context of real-life extinction events (Duncan & Young 2000; Brashares 2003; Koh et al. 2004).

Populations are experiencing rapid rates of decline globally (WWF 2018) and, given that different species are more susceptible to different types of threat, this includes populations of an ecologically diverse range of species (Ripple et al. 2017). The result is populations of species, with a variety of intrinsic traits, reaching critically low levels and potentially entering the extinction vortex (Fagan & Holmes 2006). With the aim of minimising population extirpation, it is imperative that we understand the different factors that can predispose populations to greater vulnerability at small population sizes allowing us to prioritise effort accordingly. At present only one study explicitly investigates differential robustness to the extinction vortex according to a specific trait, finding that lineages with stronger sexual selection are more robust to the vortex (Godwin et al. 2020). However, no study has investigated the influence of biological traits on response to the extinction vortex, using data from wild populations.

Of particular interest is whether certain intrinsic traits operate as scaling factors for the relationship between population size and longevity, which will have important implications for conservation planning. For example, in the context of the extinction vortex, taxa predisposed to having a weaker relationship between population size and longevity are more susceptible to abrupt extinctions and, therefore, are more imminently vulnerable to extirpation over a larger range of population sizes. In contrast, those with a stronger relationship between population size and longevity may be more sensitive to the manifold stressors of the extinction vortex and it may be more difficult to rescue the population having reached a low population size.

Body size is frequently invoked in studies relating to extinction risk and is a good candidate predictor of a populations' response to the extinction vortex for two main reasons. First, as a 'catch-all' trait (Isaac & Cowlishaw 2007; Chichorro et al. 2019), it conveniently aggregates information on life history speed and ecology in a single value. Second, it is among the most readily available species-specific trait (Myhrvold et al. 2015; Chichorro et al. 2019) with a number of databases providing body size data having been assembled to facilitate comparative studies, avoiding the time-consuming nature of amassing data from a large number of sources.

In chapter 2, I investigate how a fitness-related phenotypic trait – body size – influences a populations' response to the extinction vortex, using data from wild populations monitored to extinction. Although cases of populations monitored to extirpation are scarce, I use a contemporary assemblage of vertebrate population time-series, the Living Planet Index database (http://www.livingplanetindex.org/data_portal), to assemble a larger dataset of population extirpations than previously available (Fagan & Holmes 2006). I also collect data on mean body size and other intrinsic traits from published vertebrate life-history databases (Froese & Pauly 2000; Myhrvold et al. 2015; Oliveira et al. 2017).

Chapter 2: Paper chapter

2.1 Abstract

Understanding the dynamics of small populations is critical to conserve those species at most risk. Previous work has identified demographic and environmental factors that can mutually reinforce one-another to drive populations rapidly to extinction – a process known as the 'extinction vortex.' However, studies investigating robustness to the extinction vortex in relation to life history and ecological traits have been lacking. Here, we assemble a database of 55 vertebrate populations monitored to extirpation and perform three analyses to investigate whether a key fitness-related phenotypic trait – body size – influences how populations respond to the extinction vortex. We find support for three preexisting hypotheses of the extinction vortex and evidence that body size can alter population size scales with population longevity, which may serve as a useful feature for informing how to conserve small populations.

2.2 Introduction

The Anthropocene is characterized by an unprecedented rate of biodiversity loss driven by a number of anthropogenic stressors including climate change, pollution, habitat loss, overexploitation and the transmission of invasive species (Young et al. 2016). As populations decline in the face of these stressors the need for conservation intervention becomes increasingly important. However, conserving small populations is complicated as declining population size increases the risk of detrimental demographic processes driving populations inexorably towards extinction (Fagan & Holmes 2006). For example, individual fitness in many species is expected to decrease with population size due to Allee effects (Berec et al. 2007) and a loss of genetic diversity (Saccheri et al. 1998; Blomqvist et al. 2010). Demographic stochasticity influences small populations by increasing the annual variability in population growth rate (Fagan & Holmes 2006), which is particularly problematic in small populations as major fluctuations could lead to their extinction (Gilpin & Soulé 1986; Caughley 1994). Moreover, small populations are also especially vulnerable to direct extirpation from external drivers of mortality, such as environmental stochasticity and

random catastrophes (Caughley 1994). The concurrent presence of these processes is thought to lead to self-reinforcing, rapid and catastrophic downward spirals to extinction, so-called 'extinction vortices' (Gilpin & Soulé 1986), during which there may be little prospect of the population recovering even with intense conservation effort (Palomares et al. 2012). To identify the populations most at-risk and to make informed conservation decisions, we need to understand the factors that determine the robustness of a population to the extinction vortex.

Fagan and Holmes (2006) empirically corroborated, albeit with a small database of population extirpations, several preexisting hypotheses of the extinction vortex; specifically, that (i) time to extinction scales to the logarithm of population size, indicating that as a population declines its time to extinction decreases at an increasing rate, (ii) geometric growth rate declines as extinction nears, due to declining individual fitness and (iii) annual variability in population change increases as extinction nears, attributable to an increasing influence of stochastic factors. However, despite the compelling evidence of extinction vortex dynamics found in real-life populations, we know very little about what drives variation in species' response to the extinction vortex.

A species' intrinsic and ecological traits are often key predictors of extinction risk (Gaston & Blackburn 1995; Purvis et al. 2000; Cardillo et al. 2008), with geographic range size, life-history speed, and degree of specialization emerging as persistent indicators (Chichorro et al. 2019). However, with few exceptions (Duncan & Young 2000; Brashares 2003; Koh et al. 2004), real-life extinctions have rarely been used to infer extinction proneness in relation to biological traits (Brook et al. 2008). Similarly, using a lab-based experiment, Godwin et al. (2020) were the first to explicitly investigate how variation in a specific behavioral trait (mating pattern) can result in differential population vulnerability to the extinction vortex; though analogous studies have not been carried out on real-life population data.

Unfortunately, many of the traits identified as important predictors of extinction risk are difficult to measure, particularly in populations which are already severely reduced, meaning that it is necessary to use proxy measures of these intrinsic ecological traits. The most important among these is perhaps body size, associated with a suite of intrinsic,

ecological and anthropogenic factors that are frequently invoked in studies relating to extinction risk such as life-history speed, population density and the level of exploitation by humans. Furthermore, because of the ease of obtaining body size data and the significance of body size as a correlate of many hard-to-record population traits, it is arguably the most readily available trait available among taxa. This enhances the potential utility in predicting how small populations will respond without having to obtain more cryptic information with time-consuming and expensive data-collection procedures.

Smaller-bodied species are generally more fecund with greater intrinsic rates of growth, meaning they can recover from perturbations more quickly (Brook & Bowman 2005) and spend less time at small population sizes where there is a large threat of extirpation (Allen et al. 2017). However, slower life history speed in larger-bodied species is linked to greater resistance to both environmental (Millar & Hickling 1990; Peltonen & Hanski 1991; Sinclair 2003; Saether et al. 2013; Yeakel et al. 2018) and demographic (Jeppsson & Forslund 2012; Saether et al. 2013) stochasticity. Greater susceptibility to stochastic processes implies that populations of smaller-bodied species can be abruptly reduced to a point where the risk of extinction is acutely high (Schoener et al. 2003; Allen et al. 2017).

The potential importance of our question for conservation management are illustrated by comparing two threatened species on the IUCN Red List: the Javan rhino (*Rhinoceros sondaicus*) and Santa Catarina's guinea pig (*Cavia intermedia*). Despite having highly disparate life histories, ecological lifestyles and body sizes (~4 orders of magnitude), both species are listed as critically endangered due to their vanishingly small population sizes (criterion D: estimated total population size of fewer than 50 mature individuals) (Roach 2016; Elis & Talukdar 2020) and are therefore especially vulnerable to the extinction vortex. An influence of body size on the extinction vortex will have implications for conservation efforts.

Here, we assess – for the first time – whether body size can interact with underlying demographic processes to influence the dynamics of a population in the region of an extinction event, building upon the analysis of Fagan and Holmes (2006) with the largest dataset of wild population extirpations to date. Using wild populations monitored through

to extirpation negates the need to designate quasi-extinction thresholds, which could result in erroneous interpretations of extinction dynamics (Fagan & Holmes 2006). We use a global database of vertebrate population time series, supplemented with mean body size data from various life history databases to identify 55 populations where extirpation has been observed. We find support for the three aforementioned predictions of the extinction vortex (Gilpin & Soule 1986; Fagan & Holmes 2006) and evidence that body size influences the relationship between population size and longevity.

2.3 Methods

2.3.1 Population time series data

We obtained populations monitored to extirpation from two sources: i) the Living Planet database (LPD) (http://www.livingplanetindex.org/data_portal), containing annual population abundance data for over 25000 vertebrate populations between 1950-2019 and ii) from previously published work on the extinction vortex (Fagan & Holmes 2006). A diverse range of methods to monitor population abundance are included in the LPD, with the caveat to inclusion in the dataset being that monitoring should be reputable, appropriate for the species and consistent through time. A detailed outline of inclusion criteria for the populations in the LPD are provided by Loh et al. (2005). In some cases, complete censuses of the population were carried out, whereas in others population abundance was monitored using indirect indicators. In the absence of evidence to the contrary, regardless of the method used in population monitoring, we assume that indices of population abundance are representative of the true population size at any given point in time.

Following Fagan and Holmes (2006), we defined extirpation as a population declining to a zero-abundance count at the end of the time series and identified populations from the LPD that showed this. An important point is that the term extirpation means the population of a species ceasing to exist in a given area. However, this can arise for more than one reason such as the mortality of all individuals in a population or the remaining individuals in a population relocating to another place. Here, we do not discriminate between either possibility.

Zero-abundance counts occurring before the end of the time series might indicate a relatively low species detectability and, correspondingly, a high rate of observation error (Brook et al. 2006). To minimize the possibility of including populations that were not actually extinct and to avoid inflating annual variation in population abundance, we omitted time series where zero counts occurred and were followed by subsequent observations. In addition, we only considered populations where the time between the penultimate abundance count and the zero-abundance count (signifying extirpation) was no more than one year, so that we could ascertain the exact year in which the population went extinct. Furthermore, to avoid introducing possible bias from short time series, we only included time series with at least 10 counts of population abundance. To check whether there was a systematic bias in data quality between large and small species, we fitted a Poisson generalized linear model of number of population counts in each time series predicted by body size.

Based on these filtering criteria, we produced a dataset of 55 population extirpations of 51 different species, including two elasmobranchs, five actinopterygians, one amphibian, one reptile, nine mammals and 33 birds (Table 2.1). The individual time series in the dataset had a mean length of 16.05 (±6.68) years.

Table 2.1. A summary of all the populations in the dataset and corresponding body masses.

Population number	Species name	Common name	Class	Population source	Data type	Units	Adult body mass (g)	Body mass source
1	*Acanthurus coeruleus*	Blue tang surgeonfish	Actinopterygii	LPD	Density	Mean number of fish per 45 m165	118	FishBase
2	*Alosa aestivalis*	Blueback herring	Actinopterygii	LPD	Measure per unit effort	Annual geometric mean catch per unit effort	200	FishBase
3	*Coregonus clupeaformis*	Lake whitefish	Actinopterygii	LPD	Measure per unit effort	Catch per trawl	6848.37	FishBase
4	*Glossogobius callidus*		Actinopterygii	LPD	Measure per unit effort	Annual geometric mean catch per unit effort	4.05	FishBase
5	*Pomacanthus paru*	French angel fish	Actinopterygii	LPD	Density	Mean number of fish per 45 m38	88	FishBase
6	*Pseudacris ornata*	Ornate chorus frog	Amphibia	LPD	Full count	Breeding females	4.51	AmphiBIO
7	*Acanthiza reguloides*	Buff-rumped thornbill	Aves	LPD	Sample	Average number of birds per survey	7.7	AMNIOTES
8	*Alopecoenas xanthonurus*	White-throated ground dove	Aves	LPD	Density	Individuals/100km	111.8	AMNIOTES
9	*Ardeola ralloides*	Squacco heron	Aves	LPD	Proxy	Nests	290	AMNIOTES
10	*Calidris acuminata*	Sharp-tailed sandpiper	Aves	LPD	Full count	Individuals	67.7	AMNIOTES
11	*Calidris ferruginea*	Curlew sandpiper	Aves	LPD	Full count	Individuals	59.6	AMNIOTES
12	*Cecropis daurica*	Red-rumped swallow	Aves	LPD	Measure per unit effort	Individuals	22.225	AMNIOTES
13	*Corvus hawaiiensis*	Hawaiian crow	Aves	Fagan & Holmes (2006)	Full count	Individuals	520	AMNIOTES
14	*Corvus kubaryi*	Mariana crow	Aves	LPD	Density	Individuals/100km	247.25	AMNIOTES
15	*Dendrocoptes medius*	Middle spotted woodpecker	Aves	Fagan & Holmes (2006)	Full count	Individuals	59	AMNIOTES
16	*Galerida cristata*	Crested lark	Aves	LPD	Index	Index values	43.15	AMNIOTES
17	*Gallinago hardwickii*	Latham's snipe	Aves	LPD	Sample	Individuals	155.5666667	AMNIOTES
18	*Grus americana*	Whooping crane	Aves	LPD	Full count	Individuals	6850	AMNIOTES
19	*Gyps bengalensis*	White-rumped vulture	Aves	LPD	Sample	Individuals	4871	AMNIOTES
20	*Lanius excubitor*	Great grey shrike	Aves	LPD	Index	Index values	63.98333334	AMNIOTES
21	*Lanius minor*	Lesser grey shrike	Aves	LPD	Proxy	Breeding pairs	46.925	AMNIOTES
22	*Lanius senator*	Woodchat shrike	Aves	LPD	Measure per unit effort	Individuals	36	AMNIOTES
23	*Leuconoptopicus borealis*	Red cockaded woodpecker	Aves	Fagan & Holmes (2006)	Full count	Individuals	48	AMNIOTES
24	*Limosa limosa*	Black-tailed godwit	Aves	LPD	Proxy	Breeding pairs	306.5	AMNIOTES
25	*Malurus cyaneus*	Superb fairywren	Aves	LPD	Sample	Individuals	10.5	AMNIOTES
26	*Myzomela rubratra*	Mirconesian myzomela	Aves	LPD	Density	Individuals/100km	13.35	AMNIOTES
27	*Passer domesticus*	House sparrow	Aves	LPD	Density	Individuals/sq.km	27.7	AMNIOTES
28	*Pezoporus wallicus*	Eastern ground parrot	Aves	LPD	Proxy	No. Parrots heard calling per site visit	75.7	AMNIOTES
29	*Phalacrocorax carbo*	Great cormorant	Aves	LPD	Proxy	Breeding pairs	2200	AMNIOTES
30	*Pluvialis apricaria*	European golden plover	Aves	Fagan & Holmes (2006)	Full count	Individuals	213.25	AMNIOTES
31	*Pluvialis fulva*	Pacific golden plover	Aves	LPD	Full count	Individuals	145.5	AMNIOTES
32	*Ptilinopus roseicapilla*	Mariana fruit dove	Aves	LPD	Density	Individuals/100km	91.2	AMNIOTES
33	*Pygoscelis adeliae*	Adélie penguin	Aves	LPD	Full count	Breeding pairs	4850	AMNIOTES
34	*Rhipidura rufifrons*	Rufous fantail	Aves	LPD	Density	Individuals/100km	10.2	AMNIOTES
35	*Sterna dougallii*	Roseate tern	Aves	LPD	Proxy	Breeding pairs	112	AMNIOTES
36	*Sturnus vulgaris*	Common starling	Aves	LPD	Proxy	Nests	77.675	AMNIOTES
37	*Todiramphus cinnamominus*	Guam kingfisher	Aves	LPD	Density	Individuals/100km	61.8	AMNIOTES
38	*Tringa totanus*	Common redshank	Aves	LPD	Proxy	Breeding pairs	129	AMNIOTES
39	*Vanellus vanellus*	Northern lapwing	Aves	LPD	Proxy	Breeding pairs	218	AMNIOTES
40	*Vanellus vanellus*	Northern lapwing	Aves	LPD	Proxy	Breeding pairs	218	AMNIOTES
41	*Vanellus vanellus*	Northern lapwing	Aves	LPD	Sample	Breeding pairs	218	AMNIOTES
42	*Carcharhinus albimarginatus*	Silvertip shark	Elasmobranchii	LPD	Measure per unit effort	Encounter rate	162200	FishBase
43	*Galeocerdo cuvier*	Tiger shark	Elasmobranchii	LPD	Measure per unit effort	Encounter rate	183033.33	FishBase
44	*Alces alces*	Moose	Mammalia	LPD	Full count	Individuals	351000	AMNIOTES
45	*Glaucomys sabrinus*	Northern flying squirrel	Mammalia	LPD	Measure per unit effort	Number of captured individuals per 1000 trap days	148	AMNIOTES
46	*Lycaon pictus*	African wild dog	Mammalia	Fagan & Holmes (2006)	Full count	Individuals	24249.995	AMNIOTES
47	*Marmota vancouverensis*	Vancouver island marmot	Mammalia	Fagan & Holmes (2006)	Full count	Individuals	4750	AMNIOTES
48	*Martes zibellina*	Sable	Mammalia	LPD	Full count	Individuals	1066.7	AMNIOTES
49	*Mustela erminea*	Stoat	Mammalia	LPD	Measure per unit effort	Number of captured individuals per 1000 trap days	110.33	AMNIOTES
50	*Mustela frenata*	Long-tailed weasel	Mammalia	LPD	Measure per unit effort	Number of captured individuals per 1000 trap days	170.315	AMNIOTES
51	*Rangifer tarandus*	Reindeer	Mammalia	LPD	Full count	Individuals	101250	AMNIOTES
52	*Rangifer tarandus*	Reindeer	Mammalia	LPD	Full count	Individuals	101250	AMNIOTES
53	*Spermophilus parryii*	Arctic ground squirrel	Mammalia	LPD	Density	Density per ha	747.09	AMNIOTES
54	*Glyptemys insculpta*	Wood turtle	Reptilia	Fagan & Holmes (2006)	Full count	Individuals	968.2	AMNIOTES
55	*Glyptemys insculpta*	Wood turtle	Reptilia	Fagan & Holmes (2006)	Full count	Individuals	968.2	AMNIOTES

2.3.2 Life history data

We compiled life history data for all species in this dataset from various life history databases (Myhrvold et al. 2015; Oliveira et al. 2017; Froese & Pauly 2000), extracting data on log-transformed (base 10) mean adult body mass in kg. Additionally, where possible, we collated up to four other traits indicative of life history speed: maximum longevity, age at female maturity, number of litters per year and litter/clutch size. We log-transformed (base 10) these trait values and investigate their relationship with body mass using linear regression.

2.3.3 LMM/GLMMs

We carried out all statistical analyses using R version 3.6.1 (R Core Team, 2019). We performed three statistical analyses to investigate how population dynamics change in the region of an extinction event. For each analysis we used linear or generalized linear mixed effects models (LMMs/GLMMs) in the 'nlme' (Pinheiro et al. 2019) and 'glmmTMB' (Brooks et al. 2017) packages respectively, to account for context-specific factors that could mask the effect size of fixed effects on the response variables. We accounted for the nested random effects of our data using a mixed modelling framework, with population nested inside species. This accounts for the site-specific effects on the population dynamics and the potential effects of relatedness at the species level. As avian taxa were overwhelmingly represented in the dataset (64.71% of species), we performed our analyses on all populations together and a subset constituting only avian populations.

Years to extinction

Firstly, we assessed how proximity to extinction changed as a function of population size and the body size of the species. To make each time series compatible in the same analyses, we converted time to count backwards from extinction to produce a new variable ('years to extinction') with a consistent meaning across all populations. For an extinction vortex to be present, time to extinction is expected to change as a function of the logarithm of population size. To test this, and simultaneously the influence of body mass, we scaled the population abundance estimates for each time series between 0 and 100 and fitted GLMMs

with the structures *years to extinction ~ scaled population size + log_{10}(body mass) + scaled population size:log_{10}(body mass)* and *years to extinction ~ log_{10}(scaled population size) + log_{10}(body mass) + log_{10}(scaled population size):log_{10}(body mass)*, with a Poisson error distribution and a first-order autoregressive error structure to account for time series autocorrelation. Following Fagan and Holmes (2006), we excluded the final abundance count from each time series.

Geometric growth rate

According to the extinction vortex, as a consequence of declining individual fitness due to genetic deterioration and Allee effects, the year-to-year rate of population change (geometric growth rate) is expected to become increasingly negative at closer proximity to extinction. We calculated geometric growth rate (λ) as: $\lambda = \ln (N_t / N_{t+1})$, where N_t is the population abundance in a given year and N_{t+1} is the population size one year further away from extinction. As the logarithm of zero is not resolvable, we could not obtain estimates of a populations' final growth rate before extirpation. We fitted LMMs with the structure λ ~ *years to extinction + log_{10}(body mass) + years to extinction:log_{10}(body mass)*. A positive coefficient for population size in these models would support the hypothesis that per capita growth rate decreases with population size.

Detrended variability

As populations decline, the influence of stochasticity is expected to increase and contribute to their extinction. This should manifest itself in greater annual variability in population change at closer proximity to extinction. To investigate this, we extracted the residuals from models of the structure *λ ~ years to extinction*, squared them to remove the trend and log-transformed for normality. Therefore, these values represent the detrended annual variability *[ln(residuals)^2]* in population growth rate. We fitted LMMs with the structure *[ln(residuals^2)] ~ years to extinction + log_{10}(body mass) + years to extinction:log_{10}(body mass).* Support for the hypothesis that variability in annual population growth rate increases as extinction draws nearer in time would be found by a negative relationship with years to extinction in these models.

2.4 Results

2.4.1 Relationship between number of population counts and body size

We found no significant relationship between the number of population abundance counts and body size ($p < 0.28$; Fig. 2.1). Therefore, we find no evidence of systematic bias in data quality between small and large-bodied species.

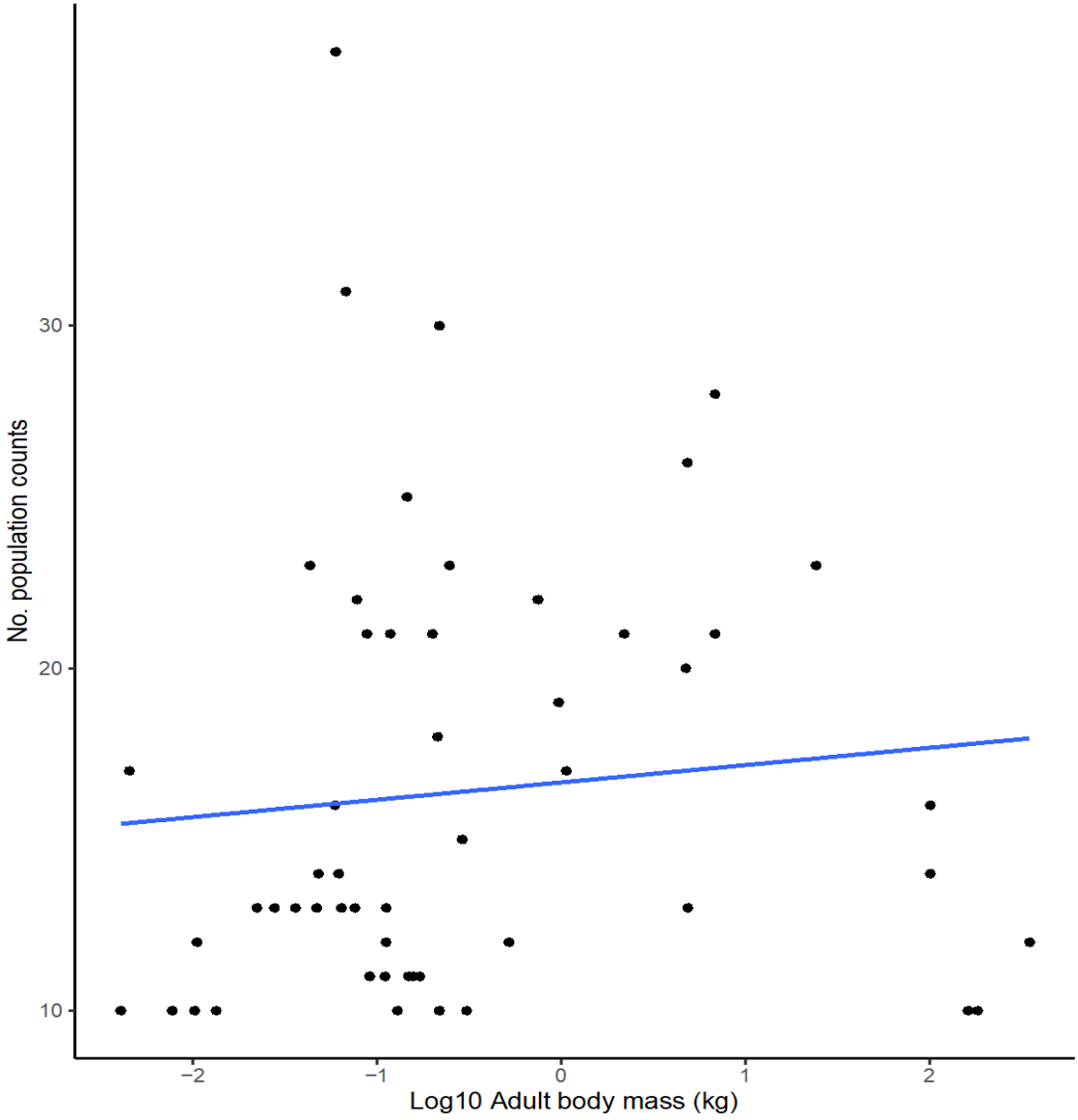

Figure 2.1 Linear relationship between logged adult body mass and the number of population counts in each time series.

2.4.2 Relationship between body size and life history traits

We found a positive relationship between body mass and maximum longevity (P = 0.02) and female maturity (P = 0.008), and a negative relationship between body mass and litter/clutch size (P = 0.005) and litters/clutches per year (P = 0.05) (Fig. 2.1). This suggests that body size in our species represents a useful umbrella trait which captures information on their life histories.

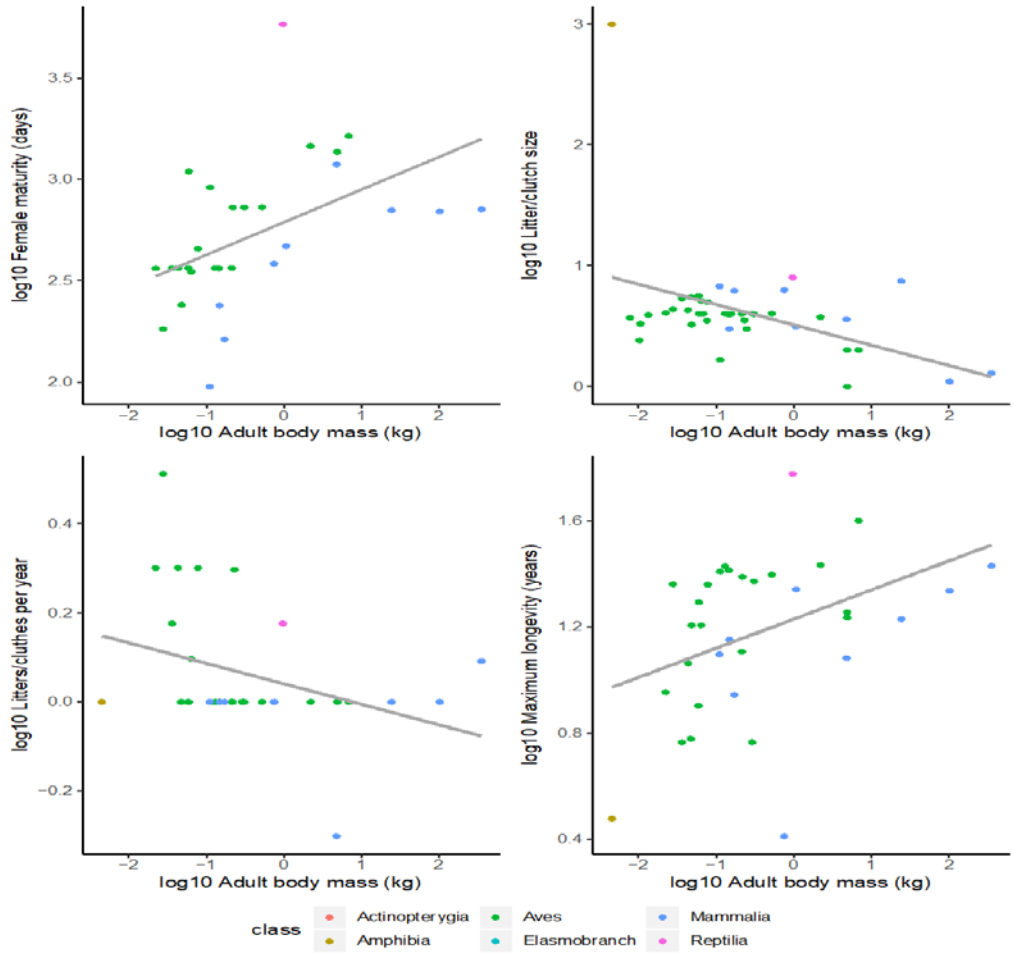

Figure 2.2 Linear relationship between logged adult body mass and four logged life history traits.

2.4.3 GLMM/LMMs

Years to extinction

In agreement with the hypothesis that populations experience a non-linear decline to extinction, for all populations and the avian subset, log-transformed scaled population size provided a significantly better fit to years to extinction than did non-logged scaled population size (Δ AIC > 2) (Table 2.2). For all populations and the avian subset, we found a

significant positive interaction between logged population size and logged body size (Table 2.3), demonstrating a stronger relationship between population size and population longevity in larger-bodied taxa.

Table 2.2. Comparison of model fit for predicting years to extinction with either logged-population size or non-logged population size.

Group	Model structure	AIC
All populations	**YTE ~ Log_{10}(scaled population size)**	**4221.4**
	YTE ~ scaled population size	4234.5
Avian populations	**YTE ~ Log_{10}(scaled population size)**	**2698.7**
	YTE ~ scaled population size	2712.6

Geometric growth rate

We found a significant positive relationship between geometric growth rate and years to extinction, with all populations and the avian subset (Table 2.3; Fig. 2.4). This supports the hypothesis that a deterioration in the population dynamics occurs during the decline to extirpation. However, there was no significant effect of body size and no significant interaction between body size and years to extinction, suggesting the rate at which each population deteriorated was independent of body size (Table 2.3; Fig. 2.4).

Population variability

For all populations and the avian population subset, we found a significant negative relationship between detrended variability in population change and years to extinction (Table 2.3; Fig. 2.5), showing that year-to-year population variability does increase as extinction is approached. There was a marginally non-significant negative effect of body size in avian populations (Table 2.3; Fig. 2.5), suggesting the annual variability in population change may have a tendency to be larger in smaller-bodied avian taxa. There was no significant interaction between body size and years to extinction, suggesting the negative relationship between population variability is the same across these species.

Table 2.3 Coefficient estimates of the fixed effects in each analysis. Uncertainties in brackets indicate standard errors. Significance is indicated by bold values and significance level is indicated by the number of asterisks.

Analysis	Model	Intercept	YTE	BM	YTE:BM	Log10(Pop)	BM:Log10(Pop)
Years to extinction							
All populations	Log10(Pop) + BM + Log10(Pop):BM	**1.32 (±0.12)*** **		-0.15 (±0.10)		**0.42 (±0.06)*** **	**0.12 (±0.04)** **
Avian populations	Log10(Pop) + BM + Log10(Pop):BM	**1.19 (±0.23)*** **		-0.11 (±0.20)		**0.59 (±0.11)*** **	**0.19 (±0.09)***
Geometric growth rate							
All populations	YTE + BM + YTE:BM	**-0.26 (±0.06)*** **	**0.02 (±0.005)** **	-0.02 (±0.05)	-0.0004 (±0.005)		
Avian populations	YTE + BM + YTE:BM	**-0.37 (±0.10)*** **	**0.02 (±0.007)** **	-0.09 (±0.08)	0.006 (±0.007)		
Detrended variability							
All populations	YTE + BM + YTE:BM	**-1.99 (±0.25)*** **	**-0.05 (±0.02)*** **	-0.16 (±0.20)	-0.02 (±0.02)		
Avian populations	YTE + BM + YTE:BM	**-2.72 (±0.40)*** **	**-0.05 (±0.02)***	-0.57 (±0.34)	-0.02 (±0.02)		

YTE: Years to extinction; BM: Body mass; Pop: Scaled population size

*P < 0.05; **P < 0.01; ***P < 0.001

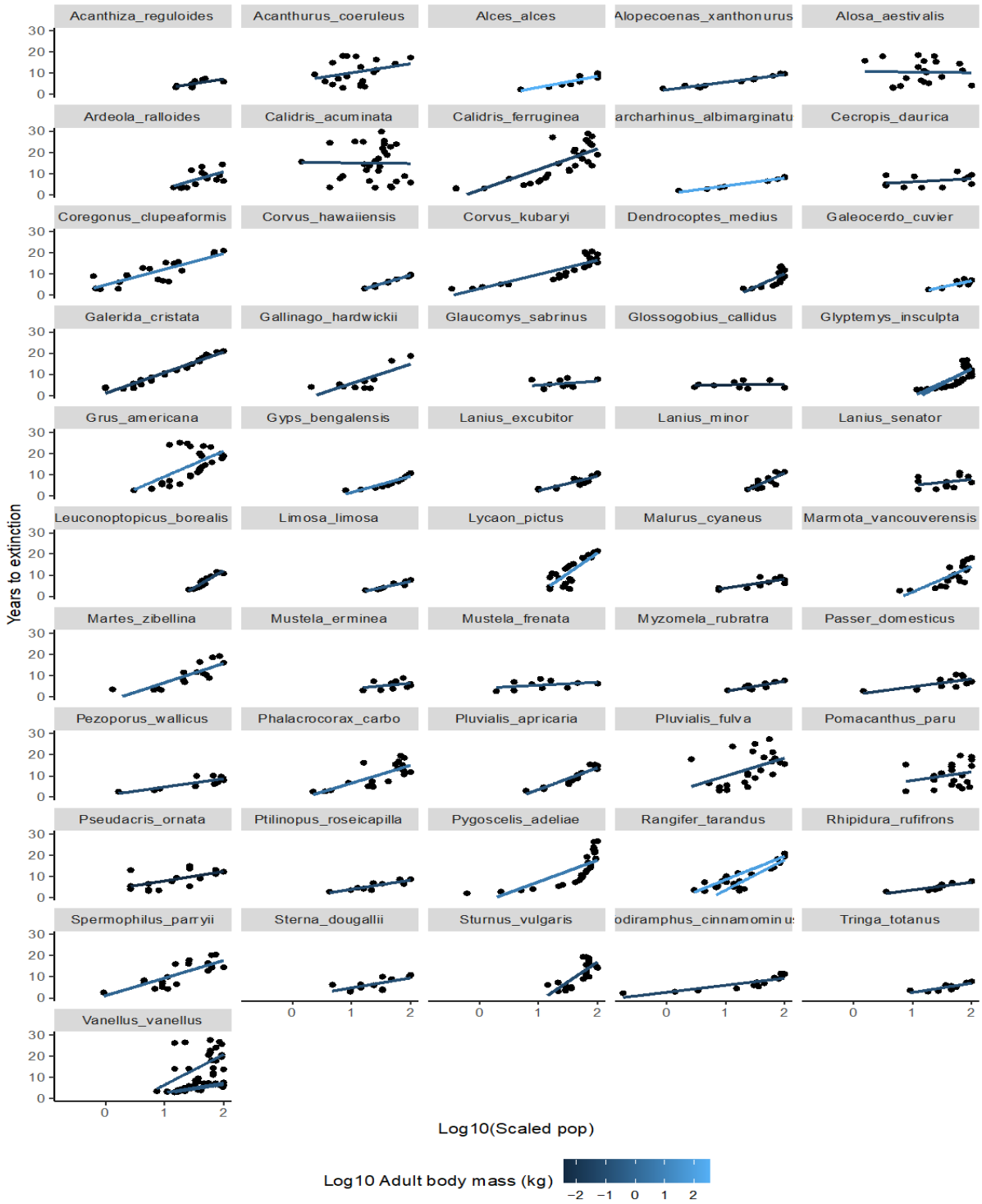

Figure 2.3 Years to extinction as a function of logged scaled population size. Plot is faceted by species binomial. Regression line colour indicates logged body size of the species.

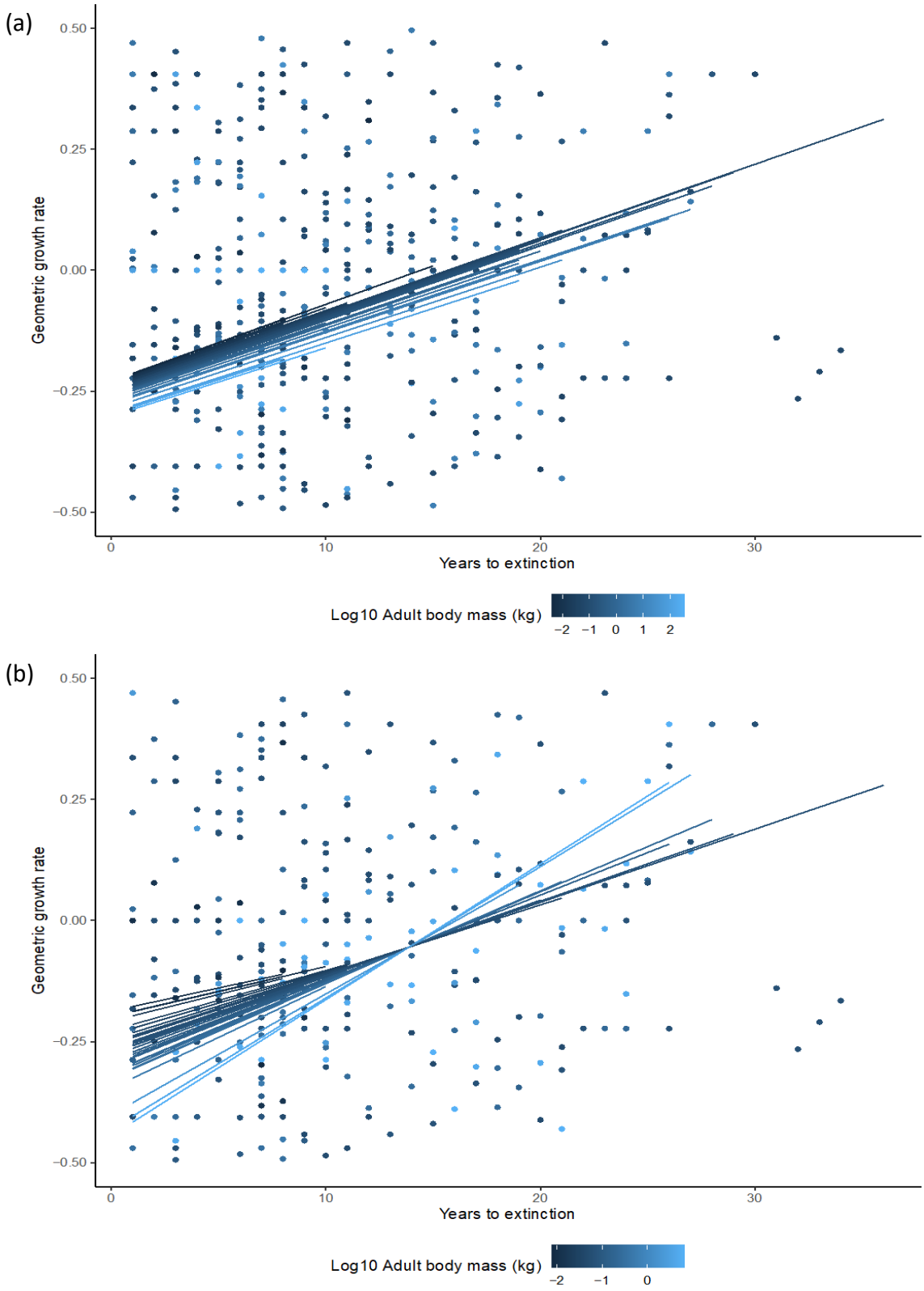

Figure 2.4 Model predictions from the second analysis (Geometric growth rate), for all a) species and b) the avian subset. Regression Line colour indicates logged body size of the species.

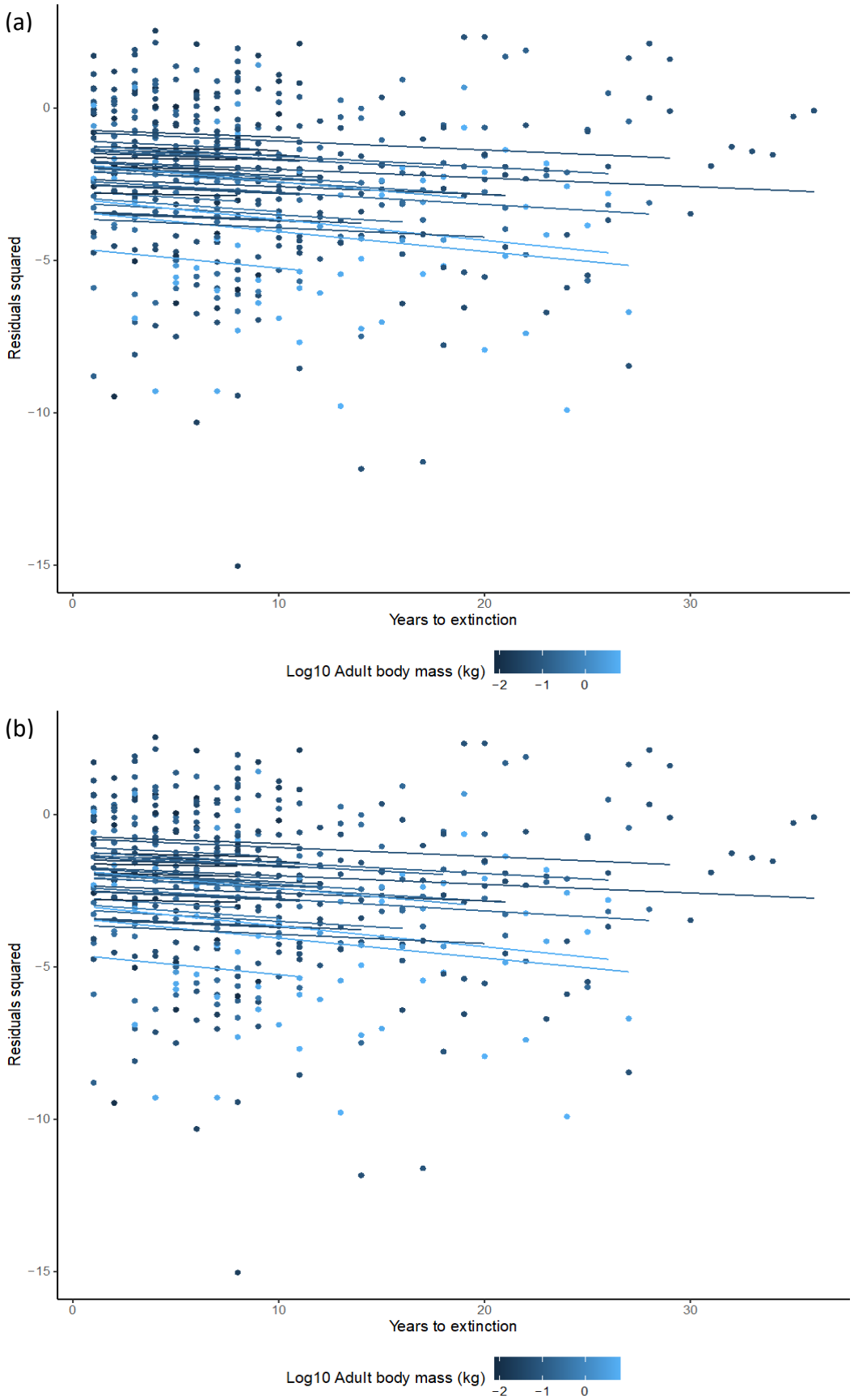

Figure 2.5 Model predictions from the third analysis (Detrended variability), for all a) species and b) the avian subset. Regression line colour indicates the logged body size of the species.

2.5 Discussion

Understanding the dynamics of small populations is critical for the effective conservation of at-risk species. Previous work has demonstrated an increase in extinction proneness in declining populations (Fagan & Holmes 2006). Here, we corroborate preexisting theoretical and empirical studies on the extinction dynamics of populations and, additionally, demonstrate that body size has an important effect on a species' response to the extinction vortex.

Reinforcing previous findings, our results show that the proximity of a population to extinction is dependent on the logarithm of population size (Table 2.2) (Lande 1993; Fagan & Holmes 2006). This suggests that the proximity to extinction decreases at an increasing rate as a population declines, indicative of an extinction vortex. Accordingly, care should be taken to maintain populations at high densities to avoid self-reinforcing spirals to extinction and to maximize the probability of long-term persistence (Fagan & Holmes 2006).

The significant positive interaction between logged population size and logged body size (Table 2.3) suggests that population size becomes increasingly important in determining the distance from extinction as body size increases. Consequently, this means that smaller-bodied taxa are generally more vulnerable to imminent extirpation than larger-bodied taxa, over a larger range of population sizes. Though it is acknowledged that extinction risk is an emergent property of the interaction between biological traits and the type of threatening process (Owens & Bennett 2000; Isaac & Cowlishaw 2007; Price & Gittleman 2007; Brook et al. 2008; Davidson et al. 2009; Ripple et al. 2017), this result may seem at odds with the frequently reported positive association between body size and extinction threat level (e.g. IUCN threat status) (Gaston & Blackburn 1995; Bennett & Owens 1997; Cardillo et al. 2005; Liow et al. 2008; Dirzo et al. 2014). However, the extinction risk of highly fecund species is tempered by naturally larger populations (Tracy & George 1992; Newmark 1995); species at the fast end of the life history speed continuum seem to be more vulnerable after controlling for the confounding effect of population size due to a greater susceptibility to stochasticity (Cook & Hanski 1995; Johst & Brandl 1997; Saether et al. 2005; Hilbers et al. 2016). That the relationship between population size and longevity is stronger in larger-

bodied taxa may also have important implications for conservation; it suggests that they exhibit stronger declines to extinction, which may be more difficult to reverse with conservation effort. Consequently, the fate of larger-bodied taxa may be more deterministic having reached low populations sizes.

According to the extinction vortex, genetic deterioration and Allee effects are expected to result in proportionally larger declines as population size diminishes (Brook et al. 2008). Indeed, we found an increase in the year-to-year per capita rate of decline at closer proximity to extinction (Table 2.3; Fig. 2.4). The implication of this is that even with conservation intervention, species that fall into the extinction vortex may struggle to be saved and require a non-linear increase in the magnitude of the change required to save a population as it moves towards extinction. Well-studied populations on the verge of extirpation support this; the decline of the Florida panther population (*Puma concolor coryi*) was only reversed after the introduction of several individuals translocated from healthy populations leading to the restoration of genetic diversity (Johnson et al. 2010). In practical terms, this emphasizes the need for early conservation intervention, with a strong focus on ensuring species do not fall into the extinction vortex. The lack of a significant interaction between years to extinction and body (Table 2.3; Fig 2.4), suggests the deterioration of population dynamics is not exacerbated in species with a specific body size. For example, inbreeding depression is a factor that is hypothesized to contribute to this deterioration, resulting in more negative growth rates closer to extirpation. This result may imply that body size does not predict susceptibility to inbreeding depression, however, in the absence of genetic data it is impossible to assess the degree to which a loss of heterozygosity contributed to each extirpation. We also know of no hypothesis that implicates, for example smaller-bodied taxa, as more susceptible to inbreeding depression.

The results of our third analysis, demonstrating a significant increase in annual population variability at closer proximity to extinction (Table 2.3; Fig. 2.5), supports the hypothesis that stochastic processes are involved in causing the extirpation of these populations (Fagan & Holmes 2006; Brook et al. 2008). There was a marginally non-significant effect of body size such that annual variability in population growth rate is generally lower in larger-bodied taxa (Table 2.3; Fig. 2.5); faster rates of reproduction in smaller-bodied species means that

their populations show a greater response to environmental and demographic stochasticity, whereas larger-bodied species are stabilised by higher survivorship and slower rates of reproduction (Sinclair 2003). We found no significant interaction between body size and years to extinction in this analysis, suggesting the increasing effects of demographic stochasticity is not exacerbated by species of a certain body size.

In conclusion, despite the large disparity in ecological and environmental contexts among the populations constituting this study, we find evidence that upon entering the extinction vortex, smaller-bodied taxa have a tendency to decline more abruptly to extinction and larger-bodied taxa decline more deterministically. In doing so, we provide one of the first studies to investigate differential response to the extinction vortex in relation to intrinsic biological traits and, to our knowledge, the first to specifically investigate this in real-life populations. The practical relevance of our findings is highlighted by the fact that species-specific data on body size is arguably the most widely available across all taxa. Our results indicate that the consequences of low population size may differ between species of disparate body size. However, they also highlight the need for a generally conservative approach to population targets for all species, irrespective of body size.

Chapter 3: General discussion

3.1 Main findings

Due to the combined effects of anthropogenic, genetic, and demographic stressors, prior to extirpation populations are thought experience self-reinforcing downward spirals known as extinction vortices (Gilpin & Soulé 1986; Fagan & Holmes 2006). To date, only one study has investigated how a populations' response to the extinction vortex can be modulated by a biological trait (Godwin et al. 2020), although this was done using a laboratory microcosm experiments due to the paucity of data on wild populations. The aim of this project was to investigate how the extinction dynamics of a population varies according to the body size of species, using data from wild populations monitored to extirpation.

To facilitate this study, I developed a dataset of 55 populations monitored to extirpation over a period of at least 10 years from a large database of vertebrate population time series and a previous study on the extinction vortex (Fagan & Holmes 2006). With this dataset, I tested three pre-existing hypotheses of the extinction vortex and, simultaneously, the influence of body size. I find support for the pre-existing hypotheses as well as evidence that body size influences the extinction dynamics of populations.

Supporting the long-standing hypothesis that populations exhibit a non-linear decline to extinction (Lande 1993), we found that time to extinction scaled to the logarithm of population size. Therefore, time to extinction decreases at an increasing rate as population size declines. Consequently, the chance of saving extinction-bound populations becomes increasingly remote the longer the extinction vortex proceeds. For the first analysis (years to extinction), the models had a significant positive interaction between logged-population size and logged-body mass. This shows that the relationship between population size and years to extinction is generally weaker for smaller-bodied species; decreasing population size affords a greater decrease in years to extinction for larger-bodied species. Previous work has shown that larger-bodied species with slower life history speeds are more robust to environmental (Peltonen & Hanski 1991; Cook & Hanski 1995; Johst & Brandl 1997) and demographic (Jeppson & Forslund 2012) stochasticity, so they are less likely to go extinct

abruptly (Saether et al. 2005). Nevertheless, that population size is more important for larger-bodied taxa suggests that they exhibit more deterministic declines to extirpation during the extinction vortex, which is likely a result of their slower paces of life and therefore slower response to perturbation. As a consequence, it may be more difficult to save larger-bodied taxa having reached low population sizes. This difference may have importance for conservation planning according to different scenarios. Specifically, when populations of small-bodied taxa become low there is a need to 'act quickly' to save them as the window of opportunity available to intervene is smaller. In contrast, for larger-bodied taxa there is a need to 'act intensely' to maximise the chance of persistence.

We found a tendency for geometric growth rate to become increasingly negative at smaller population sizes, which is the expected outcome of a combination of a decline in genetic variation and the presence of Allee effects causing a general deterioration in population dynamics (Fagan & Holmes 2006; Brook et al. 2008). We also found that variability in annual population growth rate generally increased at closer proximity to extinction, indicating an influence of stochastic processes in contributing to the extinction of these populations (Fagan & Holmes 2006; Brook et al. 2008). However, the lack of body size effects in these analyses suggest that body size is a poor predictor of sensitivity to the manifold stressors of the extinction vortex, such as inbreeding depression, Allee effects and demographic stochasticity.

Collectively, the populations herein exhibited dynamics expected under the extinction vortex. Nevertheless, we noted that some of the populations, particularly those with slower life histories, persisted at low levels for a number of years before going extinct. This 'sigmoidal' rate of population decline was also reported in a lab-based study involving experimental extinction vortices (Godwin et al. 2020), and this was suggested to be a result of genetic purging, leaving behind a few individuals that are most adept at tolerating stressors in the environment. However, unless the remaining few individuals are utilised in conservation initiatives such as translocations to augment more viable populations, a remnant population may already be defined as 'quasi-extinct'.

3.2 Limitations & future recommendations

We have found evidence that populations of smaller-bodied species experience more abrupt extinctions, with potential implications for conservation management. However, the nature of our dataset means that it has its own biases and limitations. The ultimate fate of all the populations in our analyses was extinction, and all the populations were measured in different units and had to be scaled to permit their use in the same model. Therefore, the dataset collated here is not able to address how the absolute population size at which each population entered the extinction vortex varied according to body size. By inspecting the dataset, there are clear differences between populations of different species resulting from different ecological and environmental circumstances. For example, a population of Adélie penguins (*Pygoscelis adeliae*) on Litchfield island, Antarctica, had an initial population size of around 600 breeding pairs, before declining to extinction over the 28 years. By contrast, a population of reindeer (*Rangifer tarandus*) in Banff National Park, Canada, had a population of 29 individuals before declining to extinction over the next 22 years. All else being equal, minimum viable population size (MVP) estimates are lower for larger-bodied taxa due to a lower susceptibility to stochasticity (Hilbers et al. 2016). However, the multitude of external factors may profoundly influence these estimates such that there may be a 1000-fold difference in MVP between populations of the same species (Flather et al. 2011a).

Only rarely has evidence of an extinction vortex been demonstrated in well-studied populations that are still extant (Blomqvist et al. 2009; Johnson et al. 2010; Palomares et al. 2012; Benson et al. 2019), demonstrating the difficulty in identifying populations on the brink before it is too late to intervene. Our current inability to predict when a population will enter the extinction vortex, may compromise the applicability of our findings. The ultimate fate of all populations in this study was extinction, therefore our study does not provide a complete picture of how body size influences the extinction risk of different species, per se. For example, it would be interesting to investigate whether certain intrinsic traits or environmental circumstances are associated with greater ability in recovering from small population sizes and avoiding extirpation, in the absence of conservation intervention. However, an irony is that conservation intervention for declining populations monitored over long-time frames might inhibit the number of suitable time series available for this

analysis. Instead, modelling population dynamics according to life history strategies, to devise equitable population targets based on minimum viable populations, would be more informative (e.g. Hilbers et al. 2016).

Other limitations of this study arise due to the need to balance the quality and availability of time series of populations monitored to extinction. Populations at low abundance are hard to detect (Brook et al. 2006) and population monitoring is often sporadic or generally of poor quality (Scheele et al. 2019). Therefore, although populations are disappearing globally (Ceballos et al. 2018; WWF 2018), cases of populations monitored over many years, through to extirpation, are scarce. Although our database of population extirpations is larger than that pre-existing (Fagan & Holmes 2006), the paucity of data limited the complexity of the models we were able to fit. Also, it is worth acknowledging that our dataset consists entirely of vertebrate populations. Here we build on Fagan and Holmes (2006), demonstrating the extinction vortex process in a much larger dataset of extirpations. However, this has yet to be demonstrated in other taxa such as invertebrates and plants. Additionally, whether the extinction vortex applies to certain taxa with complex social structures, such as eusocial insects, has been completely unexplored. Future work should address these knowledge gaps to give a more complete picture of extinction processes across the tree of life.

Our study focused on the influence of body size on differential response to the extinction vortex, however it is reasonable to expect other traits to influence this. For example, mating pattern has already been shown to have an effect (Godwin et al. 2020). Although regrettable from a conservation standpoint, in the years since Fagan and Holmes (2006), more examples of population extirpations have become available. It would be interesting to fit models including more traits when a larger dataset becomes available. Body size is a strong correlate of life history speed, such that larger-bodied species generally live longer and reproduce more slowly (Brook & Bowman 2005). However, ecological lifestyle also influences the evolution of life histories, orthogonal to the effect of body size (Sibly & Brown 2007; Sibly et al. 2012). For example, volant, arboreal and fossorial taxa occupy habitats characterised by a low frequency of extrinsic mortality and, correspondingly, have exceptionally slow life history speeds for their body sizes (Sibly & Brown 2007; Sibly et al. 2012; Healy et al. 2014). Also, taxa that consume abundant and reliable food sources have

faster life histories than expected from their body sizes (Silby & Brown 2007; Jones 2011). Accordingly, it is possible that two species of similar body size but with divergent ecological lifestyle, will respond to the extinction vortex differently. When data availability permits, it would be interesting for future work to investigate whether ecological lifestyle also influences robustness to the extinction vortex, independently of body size.

3.3 Conclusion

In the midst of a mass extinction event (Ceballos et al. 2015), mitigating against the loss of species and populations is a major challenge for the 21st century (Ceballos et al. 2017). As a result of diverse and ubiquitous anthropogenic stressors (Young et al. 2016), we now face the prospect of populations from a phylogenetically broad range of species entering the extinction vortex (Godwin et al. 2020). Using the largest dataset of extirpations of wild populations to date, we corroborate pre-existing hypotheses of the extinction vortex. We also find that whilst smaller-bodied species are under greater risk of imminent extinction at small population sizes, larger-bodied species exhibit stronger declines to extinction. It is clearly extremely important to preserve sufficiently large population sizes for long-term persistence, however the consequences of small population size may differ between species of different body size. Our results might inform how the optimal speed and intensity of conservation effort could be distributed between small populations, to maximise the prospects of their persistence.

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